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ORIGINAL PAPER

The influence of disturbed habitat on the spatial ecology of Argentine black and white tegu (*Tupinambis merianae*), a recent invader in the Everglades ecosystem (Florida, USA)

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Abstract The threat of invasive species is often intensified in disturbed habitat. To optimize control programs, it is necessary to understand how degraded habitat influences the behavior of invasive species. We conducted a radio telemetry study to characterize movement and habitat use of introduced male Argentine black and white tegus (*Tupinambis merianae*) in the Everglades of southern Florida from May to August 2012 at the core and periphery of the introduced range. Tegus at the periphery moved farther per day (mean 131.7 ± 11.6 m, $n = 6$) compared to tegus at the core (mean 50.3 ± 12.4 m, $n = 6$). However, activity ranges were not significantly smaller in the core (mean 19.4 ± 8.4 ha, $n = 6$) compared to periphery (mean 29.1 ± 5.2 ha, $n = 6$). Peripheral activity ranges were more linear due to activity being largely restricted to levee habitat surrounded by open water or marsh. Tegus were located in shrub or tree habitat (mean 96 %) more often than expected based on random locations (mean 58 %), and the percent cover of trees and shrubs was higher in activity ranges (mean 61 %) than the general study area (17 %). Our study highlighted the ability of tegus to spread across the Florida landscape, especially in linear disturbed habitats where increased movement occurred and in areas of altered hydrology where movement is not restricted by water.

Keywords Disturbance · Invasive species · Movement · Radio telemetry · Road ecology · Wetland restoration

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Introduction

The spread of invasive species is second only to habitat destruction as the greatest threat to global biodiversity (Wilcove et al. 1998). Land use patterns resulting from human alteration of the environment have been shown to enhance invasibility of landscapes (Hobbs 2000), thus the threat of invasive species is further compounded when combined with pervasive habitat degradation as witnessed in human-dominated systems (Vitousek et al. 1997). Therefore, identifying how altered habitats or environmental conditions contribute to invasive spread

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is imperative in planning for containment at a landscape scale (With 2002). For example, features such as roads have been implicated in aiding the invasion process by providing linear corridors that allow long-distance dispersal and penetration into previously unoccupied habitat or through habitat that would otherwise be considered unsuitable (Jules et al. 2002; Gelbard and Belnap 2003; Brown et al. 2006). Knowledge of how invaders move through and use habitat will inform patterns of range expansion and allow identification of dispersal conduits along which control methods may be most effective (Florance et al. 2011).

The landscape of southern Florida is highly altered by humans and is a hotspot for invasive species (Ewel 1986). Along with wholesale habitat loss caused by urbanization and agriculture, the native ecosystem has been degraded through altered hydrology resulting from a network of water control structures such as levees and canals (Lodge 2010). Degraded habitat, sub-tropical climate, geographic insularity, and prevalence of the exotic pet trade have resulted in large numbers of established non-native reptiles and amphibians in southern Florida (Smith 2006) with non-native lizards now outnumbering native lizard species (Meshaka 2011; Krysko et al. 2011).

The Argentine black and white tegu (*Tupinambis merianae*), also known as *Salvator merianae*, is of particular concern as an invasive reptile. As of 2014, this species was established in multiple counties in Florida including Hillsborough, Polk, and Miami-Dade (Pernas et al. 2012), and more than 600 tegus have been removed from Florida ecosystems (EDDMaps, http://www.eddmaps.org/florida/). In their native range, Argentine tegus have a broad distribution from northern Patagonia north to the Amazon forest (10°–40°S) and west to the Andes Mountains (Presch 1973; Péres Jr 2003; Embert et al. 2010; Lanfri et al. 2013). The native range encompasses tropical, subtropical, and temperate climates, with tegus exhibiting winter dormancy in response to temperature or drought (Abe 1983; Winck and Cechin 2008; Chamut et al. 2012). In their native ranges tegus occupy disturbed habitat in addition to undisturbed forested and open natural areas (Fitzgerald et al. 1991; Cardozo et al. 2012; Embert et al. 2010). The distribution and ecology of tegus in their native range suggests tegu invasion in North America could be widespread (Lanfri et al. 2013).

Invasive species are capable of negatively impacting native organisms directly through competition, predation, and disease or indirectly though alteration of ecosystem structure and function (Mooney and Cleland 2001). Tegus are omnivores with a diet that includes vegetation, fruits, carrion, small mammals, and eggs of birds and turtles (Mercolli and Yanosky 1994; Martuscelli and Olmos 1996; Escalona and Fa 1998; Kiefer and Sazima 2002; Galetti et al. 2009). Thus, there is potential that reproductive success of egg-laying species in the introduced range could be negatively impacted (Sazima and D'Angelo 2013; Mazzotti et al. 2014), especially if tegu populations are subsidized by alternative food sources (Polis and Strong 1996). Tegus also have potential to alter structure and function of ecosystems given that they are potential seed dispersers in their native range (Castro and Galetti 2004). In addition to ecosystem degradation, invasive species are known to contribute to major economic and social losses (Pimentel et al. 2005), such as those documented in the agricultural and tourism industries (Pejchar and Mooney 2009). In particular, tegus have the potential to be harmful to the poultry industry, fish hatcheries, and vegetable and fruit farms (Milstead 1961). The combined ecological, social, and economic losses make containment or eradication of this harmful species a necessity. An understanding of spatial ecology and habitat use of invasive tegus is essential in planning deployment of control tools.

Our study's main objective was to use radio telemetry to document movement and behavior of introduced *T. merianae* and to analyze habitat composition and size of activity ranges. Due to individuals in the native range showing territoriality, protandry (i.e., males emerge prior to females), greater space use, and therefore male-biased dispersal, we only tagged male tegus (Winck et al. 2011). We followed male tegus from the core and periphery of the introduced range to evaluate how space use may differ as a function of position and habitat. Tegus at the edge of an introduced range may have greater movement due to release from competition with conspecifics and access to unexploited resources beyond the current species range (Rodda et al. 2008; Urban et al. 2008). Such information on space and habitat use will also shed light on the habitat preferences of tegus and related behavior that could uncover vulnerabilities for use in tegu control by land managers.

Materials and methods

Study site and organism

We monitored *T. merianae* at the core and the periphery of the introduced and expanding population in the southern Everglades ecoregion of Miami-Dade County in Florida (ftp://ftp.epa.gov/wed/ecoregions/fl/fl_eco_lg.pdf; Fig. 1). We used *T. merianae* sightings that were reported to Early Detection and Distribution Mapping System (EDDMaps, http://www.eddmaps.org/florida/) along with knowledge of the initial release point to identify the core and periphery of the invasion in Miami-Dade County from 2008 to 2012. All tegus were within lands owned by the South Florida Water Management District. The study area of the peripheral tegus was a combination of freshwater and brackish marshes interrupted by canals created by excavating limestone to build levees which created potential corridors for terrestrial animals into the water-dominated Everglades ecosystem. The dominant vegetation in the freshwater marshes was sawgrass (*Cladium*

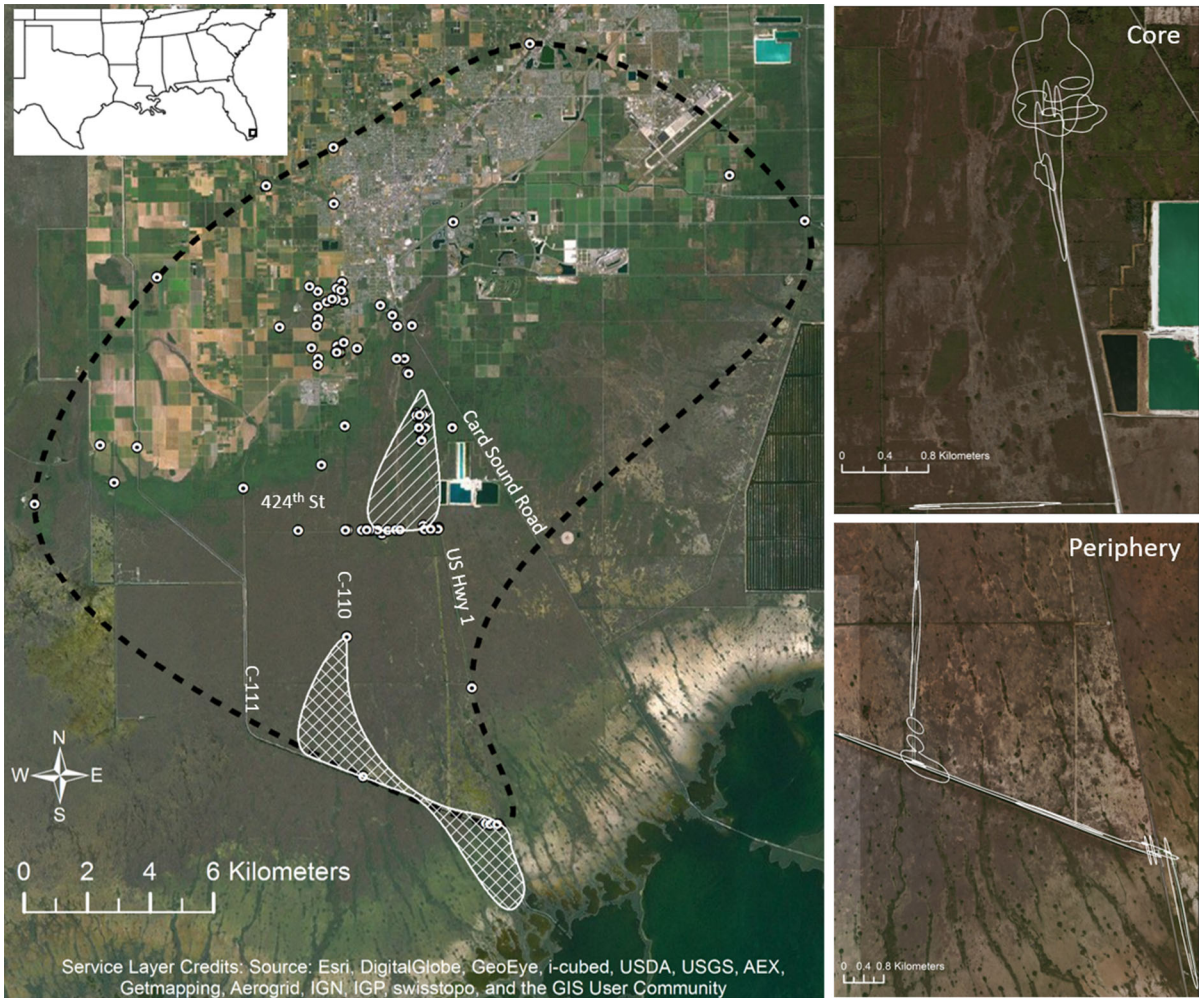

Fig. 1 Map showing the core (*white lines*) and peripheral (*white crosshatch*) study areas where Argentine black and white tegus (*Tupinambis merianae*) were radio-tracked in Miami-Dade County from May to August 2012. Tegu sightings that were reported to Early Detection and Distribution Mapping System (EDDMaps, http://www.eddmaps.org/florida/) are illustrated by *white circles* with a *dashed*, *black outline* highlighting the invasion range from 2008 to 2012. Tegu activity ranges (95 % kernel density estimates) are outlined in *white* for the core and peripheral areas. Activity ranges on the southern periphery of the invasion are more linear when compared to the core due to tegus restricting their activity to terrestrial habitat along canal levees and roads

jamaicense) interspersed with tree islands and tropical hammocks. Brackish marshes eventually transitioned into mangrove forests closer to the coast. Vegetation along elevated levees included native species such as cocoplum (*Chrysobalanus icaco*), poisonwood (*Metopium toxiferum*), buttonwood (*Conocarpus erectus*), wild lantana (*Lantana involucrata*), and eastern baccharis (*Baccharis halimifolia*), and exotic species such as Brazilian pepper (*Schinus terebinthifolius*) and laurel fig (*Ficus microcarpa*). The study area of the northern core tegus consisted mainly of wet prairie, early successional shrub habitat, and pinelands with minimal freshwater marsh. The landscape on the east side of U.S. Highway 1 was historically freshwater marsh, but due to altered hydrology and a very limited hydroperiod, the marsh is more akin to late successional grassland that is being replaced with shrubs and trees typical of an old-field. Dominant vegetation includes poisonwood, willow (*Salix caroliniana*), myrsine (*Myrsine cubana*), and Brazilian pepper. Limited developed land cover existed within the study area but areas of urban and agricultural development occurred to the north and west (Fig. 1).

The climate in southern Florida is subtropical with a warm, wet season from May to October and a cooler dry season from November to April. Throughout the year average monthly temperatures are >18 °C with an average daily minimum temperature of 14 °C in January and rare freezes. Annual average precipitation is 127–152 cm with 60 % of rain falling between June and September (Duever et al. 1994).

Tegu capture and radio telemetry

We captured tegus via live-trapping. On the periphery of the tegu distribution in southern Florida, traps were placed along a 3 km stretch of the southernmost C-110 levee and a 5 km stretch of the C-111 levee from its junction with C-110 to U.S. Highway 1 (Fig. 1). In the core of the tegu distribution, traps were placed along a 3 km stretch of access road between Card Sound Road and U.S. Highway 1 and along a 2 km stretch of SW 424th Street off U.S. Highway 1 (Fig. 1). We deployed 22 Havahart™ live-traps (model# 1079, 1089 and 1045) on the periphery and 14 traps in the core starting in March 2012 soon after tegus emerged from winter dormancy and continued to early July. We baited traps with chicken eggs and/or fruit (e.g., bananas). We checked traps daily.

We collected morphometric data including snout to vent length (SVL; cm), total length (cm), and mass (kg) upon initial and final capture. Tegus <28 cm at the end of the study may be considered sexually immature based on gametes not being found in tegus below this SVL in the Florida population (F. Mazzotti unpublished data). Radio transmitters (Holohil™ RI-2A, 8.0 g) were fitted to each tegu found in the peripheral area using beaded chain around the pelvic girdle. Tegus in the peripheral area were recaptured throughout the season to replace the harness and allow for growth. Passive integrated transponders (PIT tags) were inserted in the upper, right thigh for further identification in peripheral tegus. In the core area, radio transmitters (Holohil™ BD-2, 1.6 g) were fitted to each individual using 1.0 mm nylon coated leader line around the pelvic girdle to allow for growth and secured with barrel crimps. All transmitters comprised <1 % of the tegu body weight. Tegus were released at point of capture and radio-tracked on average every third day until they entered their brumation site, died, or were removed prior to brumation. Upon final capture all individuals were euthanized by captive bolt (American Veterinary Medical Association 2013).

Tegus were radio-tracked during the 2012 active season (March–September). Peripheral tegus were monitored by radio telemetry and motion-activated, digital trail cameras while in brumation (September–February; MA McEachern unpublished data) and subsequently captured for euthanasia via targeted trapping efforts after emerging from brumation in 2013 (January–April). At the end of August core tegus were hand captured at sunset prior to brumation for euthanization. The bulk of telemetry field work occurred in 2012 from May to August during which male tegus were thought to maintain restricted activity ranges after spring mate-searching ceased and before initiating movement to brumation sites (Noriega et al. 2002).

Space use

We restricted spatial analyses for all tegus to locations obtained between 1 May and 31 August 2012 because this is the point in the annual cycle in which long distance movements for mate searching are complete and activity ranges are thought to stabilize (Noriega et al. 2002). We calculated total distance moved (i.e., sum of all movements), average distance moved per

day (i.e., total distance moved divided by the number of days in entire monitoring period), distance per move (i.e., distance moved between subsequent locations divided by number of days between locations), maximum distance per move, and range length (i.e., Euclidean distance between the two most divergent locations). We estimated activity ranges for individual tegus using minimum convex polygons (MCP) and kernel density estimation (KDE) in the Geospatial Modeling Environment (GME) extension of ArcGIS 10.1. We estimated the number of locations needed for activity range estimation by plotting the number of locations against the 100 % MCP activity range area and evaluating the asymptote of the curves (Fig. 2). We started with five locations and increased the number of sequential locations by five until all locations were included in the MCP activity range. We included KDE as an activity range method because it shows areas with higher densities of locations by using 50 and 95 % isopleths highlighting areas of core use. In addition to these traditional estimates of activity range, we calculated linear activity range. Linear habitats were typically associated with levees along canals and therefore the linear activity range was the straight-line distance of levee used. If a tegu did not occupy a linear habitat the length and width of the MCP were summed. We used the Wilcoxon rank sum test in Program R 2.14.1 (R Development Core Team 2009) to analyze differences in space use between the core and peripheral tegus as well as by habitat affiliation. Analyses that excluded potentially immature tegus were also conducted.

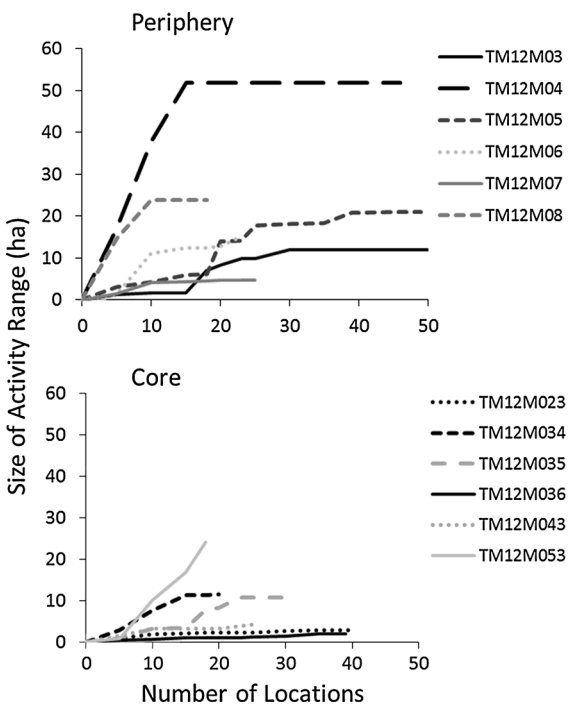

Fig. 2 Size of the minimum convex polygon (MCP) activity range as a function of number of locations for male Argentine black and white tegus (*Tupinambis merianae*) at the core and periphery of the introduced range in Miami-Dade County as of 2012. The asymptote occurs between 10 and 20 locations for most tegus, justifiying the inclusion of all 12 tegus in analyses

Habitat use

We defined the study area for the core and peripheral tegus by using 95 % KDE that included all tegu locations recorded between May and August 2012 (overall study area 3,587 ha). We categorized habitat within study areas and within the individual activity ranges using the 2008–2009 land cover/land use Geographic Information System (GIS) layer created by South Florida Water Management District modified FLUCCS classification system (http://www.sfwmd.gov). The minimum mapping unit for wetlands was two and five acres for uplands. We reduced the number of cover classes to six, including open water, human development, trees/shrubs, prairie, freshwater marsh, and saltwater habitat. Open water mainly included channelized waterways but rock quarries, holding ponds, and reservoirs were also found within the study area. Human development in the study area was restricted to correctional facilities given that roads and highways were not included as a cover class and the study area included minimal urban areas. The category of trees and shrubs encompassed Australian pine (*Casuarina* spp.) forests, mixed wetland hardwoods, and other disturbed and shrub covered upland habitats. The prairie cover class included both dry prairie and wet prairie that is occasionally inundated with water during summer. The freshwater marsh has a consistent and longer hydroperiod than wet prairie and included marshes dominated by grasses with a scattering of shrubs as well as non-vegetated wetlands. The saltwater habitat included mangrove forests, saltwater marshes, embayments, and tidal flats. We calculated expected use as the proportion of available habitat in the study area and observed use as the proportion of habitat types within activity ranges (i.e., second order habitat use). Habitat use was considered random if the

log-ratios of available and used habitat were approximately equal. Third order habitat use was considered random if the log-ratios of habitat used in the radio-tracked relocations was equal to the log-ratios of random points within a 100 m buffer of the MCP of each activity range. In the evaluation of third order habitat use we removed the development category and added a road category given that we could estimate the number of random and actual locations on roads from field data and satellite imagery of the study area. We used the "Analysis of Habitat Selection by Animals" package (adehabitatHS) in Program R 2.14.1 (R Development Core Team 2009) to run the compositional analysis as described by Aebischer et al. (1993).

Results

Tegu capture and radio telemetry

In the periphery we captured and tagged seven male tegus between 8 March and 4 July 2012 (SVL: mean 32.7 ± 1.4 cm; mass: mean 1.5 ± 0.2 kg). One male tegu died with only 11 relocations over a 47-day monitoring period and therefore was not included in the analyses. The transmitter was recovered near a number of bare vertebrae; the cause of death was not determined. A second male tegu (i.e., TM12M08) died before entering brumation but was included in the analyses. At the time of the presumed depredation event, we witnessed an odd auditory output from the transmitter, large movements in short time periods, and underground locations indicating that the transmitter may have been ingested by a large-bodied fossorial predator (e.g., python). In the core we captured and tagged six tegus between 12 March and 18 June 2012 (SVL: mean 27.1 ± 2.5 cm; mass: mean 0.7 ± 0.2 kg). Only one of the six core tegus (i.e., TM12M23) was located west of U.S. Highway 1 on SW 424th street in habitat similar to the peripheral tegus. We categorized this tegu as core for analyses due to spatial location (Fig. 1). Another tegu (i.e., TM12M34) was removed early and euthanized in July due to an injury. We included TM12M08 and TM12M34 in analyses because we had 18 and 20 relocations respectively before removal and activity ranges had reached an asymptote (Fig. 2). Tegu size at the core was not significantly different from the periphery for SVL (Wilcoxon rank sum test, $W = 28$, $P = 0.12$) and total length ($W = 28$, $P = 0.11$) and only marginally significant for mass ($W = 30$, $P = 0.05$) when comparing size upon initial capture (Table 1). The final SVL for TM12M36 and TM12M43 was <28 cm and therefore may be considered immature.

Space use

We monitored tegus for 51–120 days (mean 93.8 ± 7.8, $n = 12$) between 2 May and 31 August 2012 with 18–50 locations per tegu (mean 32.0 ± 3.5, N = 12). Average total distance moved for tegus on the periphery was 12.8 km per season with an average distance of 147.8 m per move (Table 1). The average total distance moved for tegus in the core was 4.7 km per season with an average distance of 58.2 m per move (Table 1). The mean distance moved per day (Wilcoxon rank sum test, $W = 34$, $P = 0.009$) was 2.6 times greater in the periphery (mean 131.7 ± 11.6, $n = 6$) than in the core (mean 50.3 ± 12.4, $n = 6$). The average range length and linear activity range for tegus on the periphery were 2.1 and 2.2 km respectively, whereas the average range length and linear activity range for tegus in the core was 0.7 and 1.0 km (Table 1). Mean range length was 200 % greater (Wilcoxon rank sum test, $W = 34$, $P = 0.009$) in the periphery compared to the core. The core and periphery also differed significantly in the maximum distance moved per day (Wilcoxon rank sum test, $W = 35$, $P = 0.004$). Average maximum distance moved per day on the periphery was 586.8 m, whereas average maximum distance moved per day in the core was 196.5 m (Table 1), with peripheral tegus having more long distance movements compared to core (Fig. 3). When categorizing by habitat affiliation and not spatial location (i.e., TM12M23 would be in the peripheral group), conclusions did not change and differences in movement behaviors were amplified (Table 1). When excluding the two tegus in the core that may have been immature (i.e., TM12M36 and TM12M43), conclusions did not change but differences in movement behaviors were reduced.

We estimated the MCP activity range for peripheral tegus to be 4.7–51.9 ha (mean 21.4 ± 6.7 ha, $n = 6$; Table 1) and for core tegus to be 2.0–24.2 ha (mean 9.2 ± 3.4 ha, $n = 6$; Table 1). The 95 % KDE activity ranges ranged from 3.8 to 58.6 ha (mean 19.4 ± 8.4 ha, $n = 6$) at the core and ranged from 11.3 to 46.8 ha (mean 29.1 ± 5.2 ha, $n = 6$) on the

Table 1 Space use statistics for male Argentine black and white tegus (*Tupinambis merianae*) at the core and periphery of the introduced range in southern Florida (May–August 2012)

Tegu ID	Start date	End date	Monitor period (days)	Number of locations	SVL (cm)	Total length (cm)	Mass (kg)	Total distance moved[a] (m)	Distance moved per day[b] (m)	Distance per move[c] (m)	Maximum distance per move (m)	Range length[d] (m)	100 % MCP (ha)	95 % KDE (ha)	50 % KDE (ha)	Linear activity range[e] (m)
Periphery																
TM12M03	2-May-12	30-Aug-12	120	50	35.5	94.5	1.7	17,328	144	136	468	2,860	12.0	17.6	4.1	2,863
TM12M04	2-May-12	30-Aug-12	120	46	31.0	87.5	1.3	18,546	155	177	836	2,557	51.9	33.7	7.3	2,839
TM12M05	8-May-12	30-Aug-12	114	48	30.5	89.4	1.0	18,591	163	176	615	2,417	21.0	31.5	7.2	2,493
TM12M06	14-Jun-12	30-Aug-12	77	23	26.5	77.6	0.6	10,264	133	173	693	2,647	15.1	33.7	7.9	2,646
TM12M07	17-Jun-12	29-Aug-12	73	25	34.0	96.0	1.7	6,895	94	102	519	1,203	4.7	11.3	2.9	1,205
TM12M08	4-Jul-12	24-Aug-12	51	18	34.0	101.0	1.7	5,119	100	123	390	1,050	23.9	46.8	8.1	1,432
Mean			92.5	35.0	31.9	91.0	1.3	12,790.5	131.7	147.8	586.8	2,122.3	21.4	29.1	6.3	2,246.3
SE			12.0	5.9	1.3	3.3	0.2	2,499.0	11.6	13.1	66.2	320.9	6.7	5.2	0.9	300.0
Core																
TM12M23[f]	2-May-12	29-Aug-12	119	40	28.5	78.1	0.7	11,972	101	114	394	1,085	2.9	4.8	1.1	1,085
TM12M34	7-May-12	27-Jun-12	51	20	37.4	95.2	1.4	3,653	72	82	287	1,151	11.4	22.7	4.8	1,472
TM12M35	10-May-12	31-Aug-12	113	32	29.4	80.2	0.7	3,713	33	42	146	493	10.7	17.7	3.3	938
TM12M36[g]	10-May-12	31-Aug-12	113	39	22.1	61.8	0.3	3,264	29	33	94	259	2.0	3.8	1.0	385
TM12M43[g]	23-May-12	31-Aug-12	100	25	20.4	58.1	0.3	2,072	21	26	95	420	4.2	8.8	2.0	565
TM12M53	18-Jun-12	31-Aug-12	74	18	24.6	70.3	0.6	3,472	47	52	163	813	24.2	58.6	16.5	1,753
Mean			95.0	29.0	27.1	74.0	0.7	4,691.0	50.3	58.2	196.5	703.5	9.2	19.4	4.8	1,033.0
SE			11.0	3.9	2.5	5.5	0.2	1,476.8	12.4	13.7	48.9	150.6	3.4	8.4	2.4	213.1

[a] Sum of all distances over the entire active season

[b] Total distance moved over entire season divided by monitoring period

[c] Distance moved between subsequent locations divided by days between subsequent locations

[d] Euclidean distance between the two most divergent points

[e] Total distance of linear habitat features used (e.g., levees or roads)

[f] Categorized as a tegu in the core due to position but in a habitat more akin to the periphery

[g] May be sexually immature given SVL at the end of the study was <28 cm (TM12M53 had an SVL of 29.1 upon euthanization)

periphery. Activity ranges at the core were not significantly different from the periphery for 100 % MCP (Wilcoxon rank sum test, $W = 29$, $P = 0.09$), 95 % KDE ($W = 26$, $P = 0.22$), or 50 % KDE ($W = 27$, $P = 0.18$). No changes in conclusions concerning activity ranges occurred when tegus were grouped by habitat affiliation and not spatial location. When immature tegus were excluded the differences in activity ranges were reduced with no change in the conclusions.

Habitat use

The study area was composed of 32 % freshwater marsh, 37 % saltwater habitat, 17 % trees and shrubs, 12 % prairie, 2 % open water, and <0.15 % urban development. In the core, the percentage of 95 % KDE activity range that was covered with trees and shrubs ranged from 40 to 100 % with remaining habitat composed of 0–60 % dry or wet prairie (i.e., historically freshwater marsh with reduced hydroperiod). In the periphery, habitat composition of activity ranges varied with 2–66 % trees and shrubs, 0–82 % freshwater marsh, 0–50 % saltwater habitat, 1–23 % open water, and no prairie habitat. Habitat used by tegus (i.e., 95 % KDE activity ranges) differed significantly from random ($\Lambda = 0.0014$, $P < 0.001$) with tree and shrub habitat and open water occupying a higher proportion of the activity range than what was available in the study area (Fig. 4). Habitat at radio-tracked locations differed significantly ($\Lambda = 0.12$, $P < 0.001$) from habitat at random locations (i.e., within 100 m of MCP) with tree and shrub habitat being used more often at actual than random locations (Fig. 4).

Discussion

We used radio telemetry to understand how invasive tegus move through and use habitat in the southern Everglades ecoregion. Tegus in the core and those at the periphery of the introduced range exhibited significantly different movement behaviors. Greater movement at the edge of an invasion front has been linked to

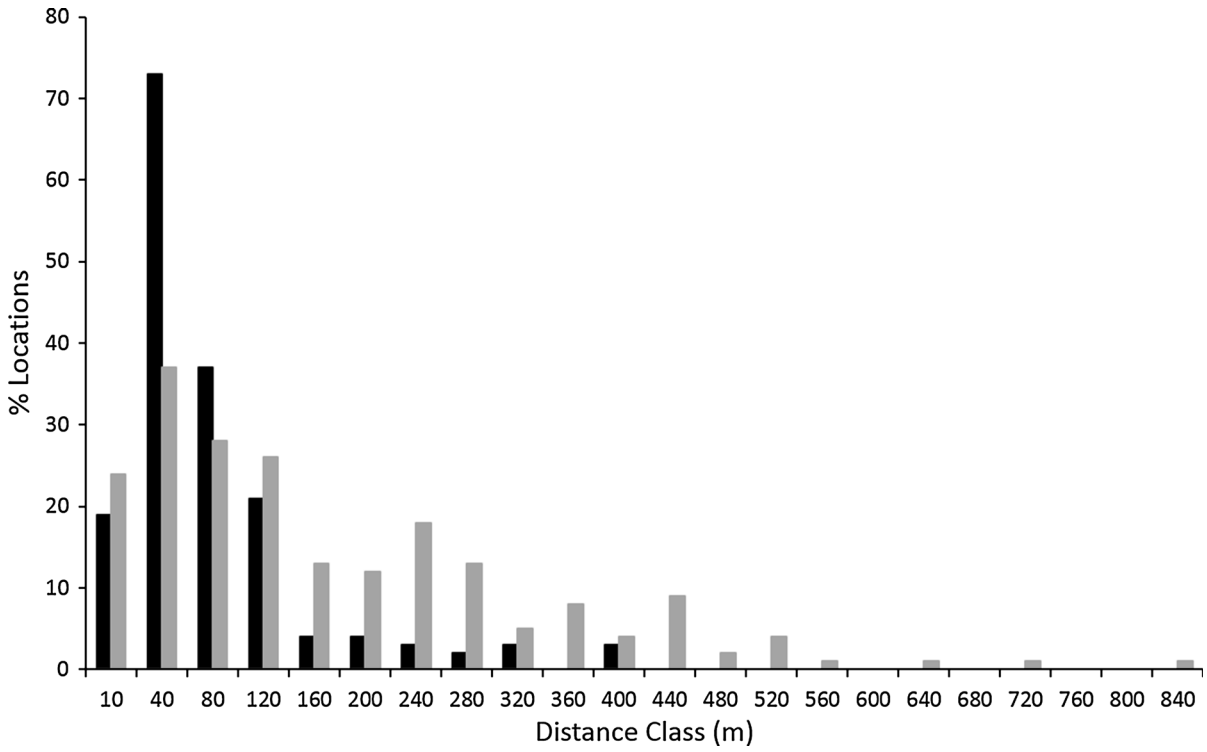

Fig. 3 Percent of radio-tracked locations in each distance class for male Argentine black and white tegus (*Tupinambis merianae*) in Miami-Dade County from May to August 2012. Core = *black bars* and periphery = *gray bars*. Distance recorded as distance moved between subsequent locations divided by number of days between relocations

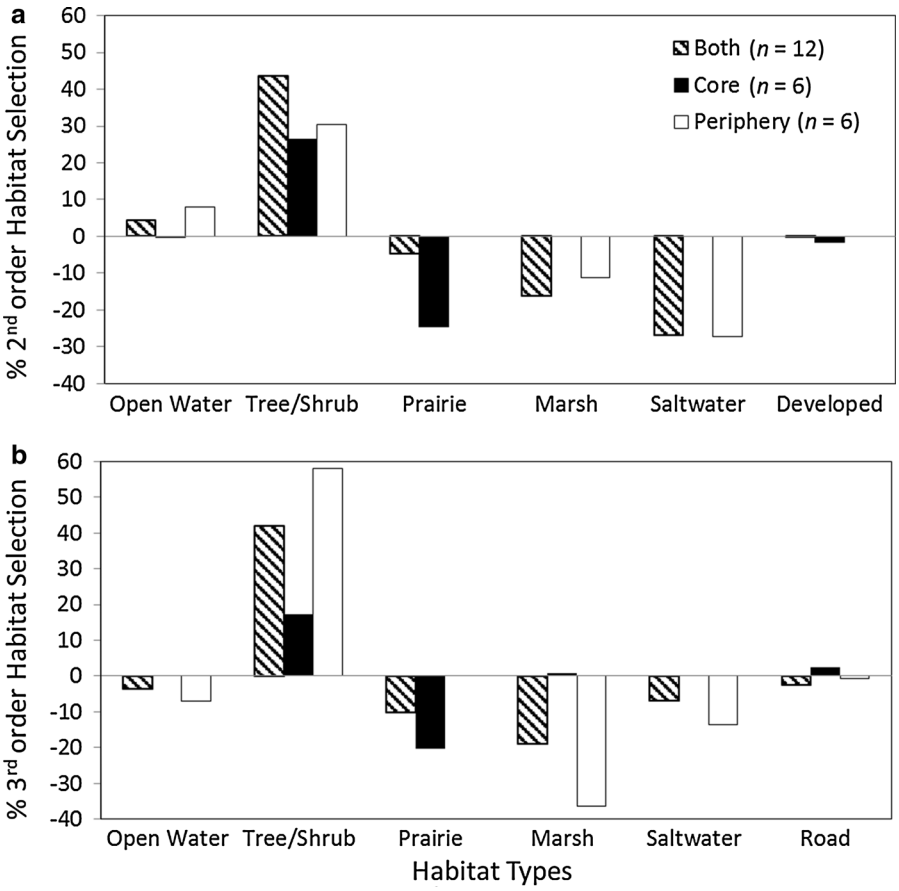

Fig. 4 **a** Percent second order habitat selection (% habitat in 95 % KDE activity range—% habitat in study area) and **b** percent third order habitat selection (% actual locations in habitat—% random locations in habitat) for male Argentine black and white tegus (*Tupinambis merianae*) at the core and periphery of an introduced population in southern Florida. Prairie did not occur in the peripheral study area, whereas freshwater marsh and saltwater habitat did not occur in the core (albeit land classified as prairie in the core was historically freshwater marsh). Road was not classified in the second order habitat selection due to limitation of the land cover classification for calculating percent habitat. *Positive values* indicate that the percent used was higher than available and *negative values* indicate that the percent used was less than what was available

selection pressure to disperse rapidly in an effort to access unexploited habitats in the brown treesnake (*Boiga irregularis*) invasion in Guam (Rodda et al. 2008) and the cane toad (*Rhinella marina*) invasion in Australia (Urban et al. 2008). Tegus were likely introduced within the last 10–15 years (Krysko et al. 2011) and are currently at a relatively small population size compared to other broad scale invasions, such that selection pressure is unlikely to be the main factor affecting movement at the range periphery at this time (Alford et al. 2009). Instead the differences could be due to larger tegus on average (e.g., mass) monitored at the periphery, but because age is unknown it is uncertain whether this demonstrates increased body condition, a preference of older males to inhabit the periphery of the introduced range, or chance due to small sample size. Nonetheless, SVL was not significantly different and when the two potentially immature tegus were dropped from the analysis conclusions did not change, suggesting that sexual maturity and size differences were not likely contributing to movement differences. In this study, the core and peripheral tegus inhabited areas that had pronounced differences in habitat composition and configuration. Therefore the difference in movement behavior between tegus in the core and periphery of their introduced range is most likely a function of habitat composition based on observed habitat preferences.

The altered landscape of southern Florida increases suitability and connectivity of the landscape for

numerous invasive and non-native species. The study area surrounding most of the core tegus could be characterized as historically freshwater marsh, but is currently more akin to late successional grassland being replaced with shrubs and trees due to an altered fire regime and shortened hydroperiod as a result of human engineering (Knickerbocker et al. 2009). It has been shown that alteration of depth, duration, and distribution of flooding has resulted in increases in invasive species in southern Florida [e.g., melaleuca (*Melaleuca quinquenervia*) and Brazilian pepper] and general tree encroachment in freshwater marshes (Knickerbocker et al. 2009; Center et al. 2012). Concurrently, the study area of the periphery is water-dominated and is a combination of freshwater marsh or brackish habitats interrupted by linear roads, canals, and levees. The network of canals and levees in southern Florida is thought to facilitate the spread of a number of invasive species including aquatic (e.g., spotted tilapia [*Tilapia mariae*]; Brooks and Jordan 2010) and terrestrial species (e.g., Burmese python [*Python molurus bivittatus*]; Dorcas and Willson 2011 and fire ants [*Solenopsis invicta*]; Stevens et al. 1999). Our study lends evidence that both types of disturbed land cover pose a problem for the potential spread of the invasive tegu given that those habitats were used in greater proportion by tegus than land cover considered natural for the Everglades (e.g. freshwater marsh).

Our analyses suggest that the human-altered nature of the landscape may facilitate dispersal of male tegus. Decreased water levels in a historic marsh create successional shrubland which is preferred tegu habitat. Without being restricted by habitat (i.e., water), tegus are capable of moving freely in any direction, a situation that is thought to increase the rate of invasive spread and lower the odds of successful control (With 2002). Although the linear nature of levees allows for identification of movement corridors and increased efficiency in control via trapping, these habitats facilitate spread into vulnerable habitats that historically would have been isolated from terrestrial invaders (e.g., Florida Keys).

The size of activity ranges provide additional evidence that habitat composition is an important factor in explaining differences in movement behavior. Although the activity ranges of the peripheral tegus are more linear compared to the core, the average size of the 95 % KDE activity range was not significantly different. In situations where tegus are restricted to linear habitat, it appears longer distances must be covered to acquire adequate area to fulfill needs for food, shelter, and reproduction compared to those in unrestricted habitat, which may increase the rate of spread along levees.

The tegus we followed had activity ranges (95 % KDE) that varied in size from 3.8 to 58.6 ha. These were greater than those reported for *T. merianae* on the coastal plain of Rio Grande do Sul State in southern Brazil, where they ranged from 0.05 to 26.44 ha (Winck et al. 2011). The differences in reported activity ranges are likely due to methods, given that the Brazilian study did not use radio telemetry, had an average of only 15 sightings per individual, and followed tegus in different seasonal timeframes (Winck et al. 2011). However, our activity range estimates are similar to those of the closely related red tegu (*Tupinambis rufescens*) in the Bolivian Chaco that range from 16 to 54 ha (Montaño et al. 2013). Activity ranges of similar size in the native and introduced range further suggest that increased movement at the periphery of the range is a function of linear habitat restrictions, which requires longer movements to reach the average activity range size and fulfill daily needs.

In both native and introduced ranges tegus are known to inhabit disturbed areas such as ditches, fencerows, open agricultural fields, and urban areas (Fitzgerald et al. 1991; Krysko et al. 2011; Sazima and D'Angelo 2013; Embert et al. 2010). Our study area contained <0.1 % urban areas and no open agricultural land and therefore does not inform predictions of use in these habitats by invasive tegus. In this study, we were able to identify preferred habitat of introduced tegus as that dominated by trees and shrubs, the same habitat that has been shown to be preferred in their native range (Cardozo et al. 2012). Tegu activity ranges also contained a higher percentage of open water than what is available in the study area but this can be attributed to activity occurring on levees adjacent to canals. Shrubby habitat is prevalent in disturbed areas and can be found along levees and roads as well as in historic freshwater marshes that are changing to successional shrubland habitat due to diverted water flow. Although known to swim, male tegus did not often penetrate into the adjacent fresh or salt water marshes, but were sometimes found in open grassland habitat or open disturbed areas if available. This suggests tegus are not confined to woody habitat

but may be restricted by presence of water and associated vegetation in southern Florida. In their native range, tegus are habitat generalists and are resident in open, xeric biomes (e.g., Caatinga, Cerrado, and Chaco), which stretch from north, central Argentina to northeast Brazil as well as open areas in the forested Amazon and Atlantic rainforest regions in Brazil (Péres Jr 2003; Embert et al. 2010; Lanfri et al. 2013). Tegus may prefer woody habitat in southern Florida because this habitat type is indicative of areas above the water line that also provide sufficient forage from abundant rodent populations and shelter within interconnected burrows (Krysko 2002).

In their native range, tegus have been shown to be resilient to market harvests (Fitzgerald et al. 1991; Mieres and Fitzgerald 2006), which suggests that once established the control of invasive tegus in southern Florida will be a challenge. Designing management plans to control populations of invasive tegus requires an understanding of how landscape composition and hydrology influences space use patterns and distribution. Human alteration of the Everglades ecosystem has added to the vulnerability of the landscape for invasion by tegus through increased terrestrial habitat and creation of corridors into water-dominated habitats. The limited movement of tegus into water dominated habitats supports placing traps along levees and canals to maximize catch, whereas large tracts of disturbed habitat may require more traps per area or a more effective bait to draw in tegus from further distances. Although intensive trapping to contain and reduce tegu populations will be necessary at the local scale, landscape scale tools are essential once the population has exceeded that in which manual labor through trapping or shooting will be effective. The affinity of tegus for disturbed, terrestrial habitat suggests that the restoration of a more natural hydrological regime may decrease the area of suitable habitat for tegus. The Comprehensive Everglades Restoration Plan (CERP; http://www.evergladesplan.org/) considers the removal of select canals and levees to improve ecological function of the southern Florida ecosystem while adding additional levees to the system. These removals and additions could function to limit and expand the spread of invasive tegus, respectively. If habitat is managed at a broad scale to reflect a more natural hydrological and fire regime, the distribution of tegus may be decreased while simultaneously impacting other invasive species and increasing the efficiency of invasive species management (Marvier et al. 2004).

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